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# A PROPOSED TERMINOLOGY FOR THE TYPES OF DIAPAUSE

## OCCURRING IN THE ORDER LEPIDOPTERA

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Diapause, a condition of suspended growth and development, is frequent among animals, and serves the prime purpose of tiding the organism over unfavorable environmental conditions. Certain animals suspend activity in direct response to changes in stimuli such as temperature, then become active again as soon as normal conditions prevail. True diapause, however, is of a more complex nature.

The physiological cause of diapause is believed to be the temporary absence of the hormones of growth and development. This cessation of hormonal secretion is usually brought about by stimuli in the environment, such as changes of photoperiod, temperature, nutrition, and possibly humiity. In true diapause there is a lapse of time which is specific, before the secretory cells resume producion of the hormones, so that the diapause lasts for some time. It is eventually ended, or broken, by another environmental stimulus, after which the production of hormones is resumed and growth and development continue.

An alternate explanation of diapause is that suggested by Roubaud, which postulates an inhibitory substance, produced by a sort of developmental fatigue. According to this hypothesis, this inhibitory substance is removed during diapause and growth resumes when all of the inhibitory factor is removed. This explanation seems to be based entirely on hypothesis. The explanation of the hormonal control of diapause, on the other hand, is supported by experimental data.

There may also exist a type of diapause that intervenes more or less automatically, as in the case of certain strains of the Silkworm, *Bombyx mori* (L.), which exists in univoltine, bivoltine, and tetravoltine strains. It should be mentioned, however, that external triggering stimuli have been reported for at least the bivoltine strain.

Diapause, once established as a part of the life history of a species, appears to be genetic, and a characteristic of that species. However, not all populations of a species need have identical types of diapause. Masaki, reporting on the Cabbage Moth, *Barathra brassicae* (L.), in Japan, found that the northern strains enter diapause on the basis of a short photoperiod. Southern strains enter a summer diapause on the basis of a long photoperiod, then the same strain enters a winter diapause when acted upon by the short photoperiod of the fall days.

Species without diapause may be regarded as of tropical origin, and to be imperfectly, or not at all, cold-adapted. Species with a true diapause fall into several groups, one treatment of which will be considered below.

Species without a diapause tend to be holodynamic and multivoltine. Species with a diapause are heterodynamic, but with a possibility of variable voltinism. In univoltine species there is always a diapause which not only carries the individuals over unfavorable conditions, but also serves the important function of synchronizing the individuals during the limited reproductive period. Bivoltine species, and possibly also certain multivoltine species, may be similarly synchronized in the first brood of the year.

Length of diapause varies greatly in different species. It may be but a few weeks, as in the arctiid moth *Arachnis picta* Pack., or last for the major part of the year, as in the eriocraniid moth, *Mnemonica cyanosparsella* Williams.

Diapause may occur in any stage of a life history. However, I have not found any instances of true diapause in adults of Lepidoptera.

In selecting terms to apply to the several types of diapause, I have used the root, *-pause*. The adjective *pausic* is used to denote a species that has a diapause. The adjective *apausic* is used to denote species without diapause. The root, *-pausic*, with certain prefixes, is used to qualify the various subsidiary types. It is proposed that diapause be classified under the following headings:

I. Apausic species — without true diapause in any stage of development.
   A. Holodynamic species — reproducing throughout the year. Such species must live where the climate is favorable all the year, or must move to a locality with favorable conditions upon the onset of unfavorable

weather. Such species are presumably of tropical origin. Such species, if they invade temperate and northern regions, can do so only during the warmer parts of the year. They either must move south with the coming of cold weather, or die. The migrations of the Monarch Butterfly, *Danaus plexippus* (L.), appear to involve this type of behavior.

B. Pseudoheterodynamic species — tending to become inactive in the adult stage when they meet unfavorable conditions. Such insects may "hibernate" as adults, but return to normal activity when favorable conditions return. Examination of such adults indicates that they are not in true diapause. Rather, they exhibit a type of akinesis or suspended activity as a direct response to unfavorable conditions. If so-called hibernating individuals of *Nymphalis antiopa* (L.) are brought into a warm room, they return to activity in a short time. If placed in a refrigerator, they soon become inactive again. Such individuals can be alternately chilled and warmed a number of times without apparent permanent injury. It may be postulated that such are temperate species of ultimately tropical origin which have become adapted to cold conditions without developing a true diapause.

In the southwestern part of the United States, *Cynthia cardui* (L.) and *Cynthia annabella* Field behave similarly in the larval stage. If reared indoors at a standard temperature, *C. annabella* will reproduce holodynamically. Under outdoor conditions, the winter brood at San Jose, California, is longer or shorter in development in direct response to temperature. During the winter, larvae may be found in various instars.

II. Pausic species — with a true diapause in some stage of life history.

A. Hiemopausic species — with diapause during the winter months.

As far as known, this type of diapause is triggered either by lowered temperature or by reduced photoperiod. Dawson (1931) found that if the last stage larvae of *Antheraea polyphemus* (Cramer) were exposed to reduced temperatures for about a week, the resulting pupae went into diapause. Williams (1946-

47) found that if pupae of *Hyalophora cecropia* (L.) were kept at a standard temperature the diapause lasted five months or more. If these pupae were chilled the diapause would break in a few weeks. Thus the diapause may be initiated by reduced temperature, and broken by a further cold shock. Williams found that brains of chilled pupae transplanted into unchilled pupae, caused the diapause of the unchilled pupae to break. It seems clear that the resumption of activity by the neurosecretory cells of the brain is responsible for the breaking of diapause in *Hyalophora*. It has been shown further that the brain hormone has an effect on the thoracic hormone, and the *Hyalophora* pupae, after coming out of diapause, went directly on to imaginal development.

The term, *thermopausic*, might be used for such instances where temperature is known to be the controlling stimulus.

Certain species have been found to enter diapause following reduced photoperiod. The Spruce Budworm, *Choristoneura fumiferana* (Clem.) has been found to do so. A rather interesting case is that of the bivoltine strain of *Bombyx mori*. Ovipositing females of this strain, if subjected to a long photoperiod, will lay diapausing eggs. The Oriental Fruit Moth, *Laspeyresia molesta* (Busck), enters diapause in response to reduced photoperiod. The northern populations of the Cabbage Worm, *Barathra brassicae* in Japan were found to do so by Masaki. The term *photopausic* might be useful to apply to species which have the diapause triggered by photoperiod, but as has been mentioned previously, not all of these would necessarily be hiemopausic.

Hibernation is a rather loose synonym of hiemopause, but as has been discussed above, certain species are said to hibernate when not in true diapause.

B. Aestivopausic species — with diapause during the warm part of the year.

This type of diapause seems to be frequent in the mediterranean climate of California, which is characterized by a winter rainy season, followed by a long dry season that lasts until the following fall. The triggering mechanism for summer diapause seems not to be known for many species. As noted above, Masaki found it to be lengthened photoperiod for the southern Japanese strain of the Cabbage Moth.

I have found rather numerous examples of summer diapause among moths in the San Francisco Bay region. *Coleophora viscidiflorella* Wlsm. diapauses inside its case during the summer. The arctiid *Arachnis picta* Pack. undergoes a larval diapause during the hotter part of the year, and when fall rains come, it pupates and soon emerges as an adult, without further feeding. The noctuid moth, *Dryotype opina* (Grt.), and a percentage of individuals of the geometrid *Prochoerodes truxaliata* (Gn.), have a long diapause in the pupal stage. Specimens of *Drytype opina* that pupated in April and May emerged as adults in October, after the first fall rains. It must be pointed out that the triggering mechanism that initiates diapause has not been found for these species.

C. Autopausic species — diapause apparently occurring automatically, the triggering mechanism either entirely genetic, or so far not known.

The univoltine strain of the Silk Moth has a diapause between each brood. It has been suggested that this occurs "automatically". If this be true, it should follow that it is a proprioceptive stimulus that triggers the diapause. However, in such species there may be another triggering stimulus that has so far escaped detection.

D. Holopausic species — diapause very long, beginning in one season and lasting through one or more subsequent seasons. Neither triggering stimulus nor breaking stimulus clearly understood at present.

This category is more or less a matter of convenience, to include species not clearly belonging to any of the other groups, and presenting some characteristics that are different.

Species with a long diapause in the egg stage are included here. The Tailed Copper, *Lycaena arota* (Bdv.), lays its eggs in June. These do not hatch (in the sense of eclosion) until the following spring, though the larvae may develop in the shell some time before they eclose. Several species of *Satyrium* (*Strymon* auct., part.) have rather similar life histories. It is noteworthy that the food plants of these species usually have fully grown, tough, unpalatable leaves at the time the eggs are laid, and that eclosion of the larvae coincides with the growth of tender leaves the following spring.

Several groups with long larval diapause are placed here. *Plebejus icarioides* (Bdv.), *Hesperia* spp., *Ochlodes* spp., and *Euphydryas* spp. may be mentioned. All of these agree in having

eggs that hatch soon after oviposition. The first instar larvae of some of these feed for a short time, then enter a diapause that lasts until the following spring, as in the case of *Euphydryas*. Or the larvae may diapause in the first instar, as is the case with *Ochlodes sylvanoides*.

*Mnemonica cyanosparsella* Williams, and apparently other members of this genus, present a remarkable condition. This species is dependent during its larval development on a critical stage in the growth of its food plant. As a larva it is a miner in the leaves of *Quercus agrifolia* Nee, the Coast Live Oak. The length of its larval development coincides with the period of new leaf growth. The egg stage is brief, the larval development rapid. The mature larva enters the soil and spins a cocoon in a cell there. The remaining ten months or so of the year are spent in diapause as a mature larva. The pupal period is quite short.

Certain species living in the sonoran and chihuahuan deserts present adaptations that are difficult to interpret. This may be because few workers have studied them in detail. The Lepidoptera of this region appear to have mechanisms that adjust their life cycles to the irregular summer rains that occur in this climate. The adults of certain species appear very shortly after rains. This would indicate that these species are in the pupal stage prior to the rains. Adults of certain other species appear some time after the rains. In some species this may be due to a diapause in the larval stage. *Euphydryas* is apparently facultatively double-brooded in parts of Arizona in certain seasons with exceptional rainfall.

In almost any region there are species that appear as adults on what has been termed a "time clock" basis. Such species emerge at nearly the same time each year regardless of weather, and may appear as adults during the driest season of the year. Some of these, such as the Agave-feeding *Agathymus*, feed in the larval stage on perennial plants little affected by ordinary changes in weather. Others, such as members of the genus *Hesperia*, feed on perennial grasses and are adjusted to the growth of these plants in relation to winter rainfall. Adults of *Hesperia harpalus* (Edw.) and *Apodemia mormo* (F. & F.), appear in the Inner Coast Ranges of California during the dri est part of the year.

E. Nutripausic species — diapause triggered by poor quality or reduced quantity of food.

Certain species have been found to enter diapause in re-

sponse to insufficient nutrition. Steinberg and Kamensky (1936) found that *Loxostege sticticalis* (L.) could be made to enter diapause by unfavorable nutrition, even when this occurred early in the life of the larvae. However, this diapause could be prevented if the temperature was kept above 32° C.

The study of diapause presents a number of complex and interesting problems. For example, strains of one species may have different types of diapause, and even in one strain, two types of diapause may occur, each with a different environmental stimulus as the trigger.

Summary: An attempt is made to explore some of the types of diapause found in the Lepidoptera, and to offer a tentative terminology by which to refer to them. It is certain that this attempt is subject to revision as more information is obtained. Nevertheless, it is hoped that this treatment will serve the useful purpose of providing a stimulus for future work.

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